A Revision of *Dianthidium* Subgenus *Mecanthidium* Michener (Hymenoptera: Megachilidae)

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Abstract.—The resin bees of Dianthidium subgenus Mecanthidium Michener are revised. Three species, all endemic to Mexico, are recognized: D. snellingi Tanner and Griswold, sp. nov., from Jalisco, D. zapotecum Tanner and Griswold, sp. nov., from Oaxaca and Chiapas; and the highly variable D. macrurum Cockerell from central Mexico. Dianthidium sonorum Michener is regarded as a new synonym of D. macrurum. A key to the species is provided.

Among the more interesting bees in the genus Dianthidium Cockerell (Hymenoptera: Megachilidae) are large reddishbrown bees of the subgenus Mecanthidium Michener. These uncommon bees, endemic to Mexico, have been recorded from the coastal states of Nayarit, Jalisco, and Colima, east into Morelos, and in the southern state of Oaxaca. Little is known about their floral host preferences or natural history, aside from nesting habits (Parker 1977). Mecanthidium was originally placed in Paranthidium Cockerell due to the long, oblique apical margin on the female mandible. Later, based on shared synapomorphies (see below), Griswold and Michener (1988) transferred Mecanthidium to Dianthidium. The placement in Dianthidium is also supported by similarities in nesting habits with other subgenera of the genus (Parker 1977). Nests are primarily made of tree resins (Parker 1977); in D. macrurum Cockerell, nests are built in crevices (e.g., crevices between rocks) using small pebbles held together with resin. There can be multiple stories of cells within a single nest, but the orientation and arrangement of cells is variable.

Roy Snelling had recognized a new species in this group and sent it to Terry Griswold.

Here, in revising this distinctive and little known group of resin bees, we wish to recognize his significant contribution to the taxonomy and systematics of bees.

MATERIALS AND METHODS

Pinned specimens of all included species were examined with a Motic K-series stereomicroscope. Genitalia were dissected and illustrated using a camera lucida. Morphological terminology follows Michener (2007) including use of the term "preomaular area" for the anterior face of the mesepisternum, which in *Mecanthidium* is dorsally set off from the lateral face by the omaular carina. We use the abbreviation T1, T2, ... T7 to denote metasomal terga 1, 2, ... 7, and S1, S2, ... S6 to denote metasomal sterna 1, 2, ... 6. Plumose setae refer to setae with branches longer than the width of the central shaft.

Institutions.—

BBSL U.S. National Pollinating Insect Collection, USDA-ARS Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah, USA.

CASC California Academy of Sciences, San Francisco, California, USA.

CISC Essig Museum of Entomology, Department of Entomological

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Sciences, University of California, Berkeley, California, USA.

LACM Insect Collection, Los Angeles
County Museum of Natural
History, Los Angeles, Califor-

nia, USA.

NMNH National Museum of Natural History, Washington, D.C., USA.

Dianthidium (Mecanthidium) Michener

Paranthidium subg. Mecanthidium Michener, 1942. N. Y. Entomol. Soc., Jour. 50: 278. Type-species: Paranthidium (Mecanthidium) sonorum Michener.

Dianthidium subg. Mecanthidium Griswold and Michener, 1988. Jour. Kansas Entomol. Soc. 61: 33.

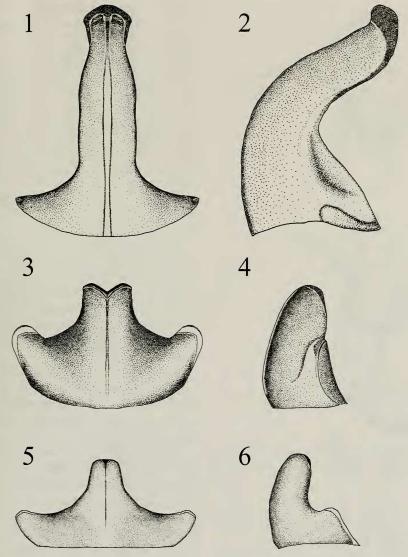
Diagnosis.—Mecanthidium is readily distinguished from all other Mexican Anthidiini except Aztecanthidium Michener and Ordway by its reddish brown color (without or with indistinct yellow bands on the terga). From Aztecanthidium it differs by the absence of a preoccipital carina, pronotal lobe lamellate and widest behind middle, and the presence of a postspiracular fovea on the propodeum. Males can be distin-

guished from *Paranthidium*, *Aztecanthidium*, and other *Dianthidium* by the presence of an elongate apical process medially on T7 well exceeding lateral processes when these are present (Figs. 1–6), and large medial transverse ridge along S3 (Figs. 7–9). Females of *Mecanthidium* differ from *Aztecanthidium* and other *Dianthidium* in the straight cutting edge of the mandible without teeth and without a preapical notch.

Remarks.—Mecanthidium was originally placed in the genus Paranthidium (Michener 1942), and later transferred to Dianthidium (Griswold and Michener 1988) based on the following shared synapomorphies: 1) feltlike setal patches present on the posterior margin of the metanotum lateral to the metanotal pit; 2) scutum with transverse anterior crest or angle separating its vertical anterior margin from the horizontal dorsal surface; 3) pronotum lacking a horizontal dorsal surface; 4) tegula as wide as long, with the widest point behind the middle of the tegula; and 5) the impunctate tergal margins ending at the side of the metasoma. The felt-like setal patches and transverse anterior crest in Mecanthidium are not as well developed as in other Dianthidium.

KEY TO SPECIES

1.	Males
-	Females
2.	T7 with apical process short, approximately ½ the total length of tergum (Figs. 3, 5);
	penis valves not concave apically, not forming opening (Figs. 12, 14)
-	T7 with apical process long, fingerlike, length much greater than ½ the total length of
	tergum (Fig. 1); penis valves concave apically forming distinct opening
	(Fig. 10) macrurum Cockerell
3.	S3 with large, impunctate, transverse process situated medially, anterior surface of
	process concave and vertical as seen in profile (Fig. 8); medial process of T7
	bifurcate (Fig. 3) snellingi sp. nov.
-	S3 with small, punctate, transverse process, anterior surface oblique as seen in profile
	(Fig. 9); medial process of T7 truncate (Fig. 5) zapotecum sp. nov.
4.	Dorsal margin of preomaular area concave; lateral margin of axilla extending beyond
	line created by scutum and scutellum zapotecum sp. nov.
~	Dorsal margin of preomaular area not concave; lateral margin of axilla forming
	contiguous line with scutum and scutellum macrurum Cockerell



Figs 1–6. Male T7 of Dianthidium (Mecanthidium) in dorsal (1, 3, 5) and lateral (2, 4, 6) views. D. macrurum: 1, 2; D. snellingi: 3, 4; D. zapotecum: 5, 6.

Dianthidium macrurum Cockerell

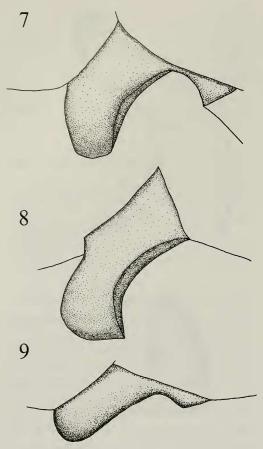
Dianthidium macrurum Cockerell 1913. Annals and Magazine of Natural History 8(xii): 107. Holotype male, Mexico (NMNH, #16226). Paranthidium (Mecanthidium) sonorum Michener 1942. Journal New York Entomological Society 50: 278. Holotype male, Mexico, Sonora, Estrella (CASC, #06682). NEW SYNONYMY

Diagnosis.—Dianthidium macrurum is readily identified by the greatly elongate medial process extending from T7, with a

dorsal carina running along the length of the tergum (Figs 1–2). In lateral view, the penis valve appears broad or swollen apically. The apical interior margin of the penis valve is concave forming a pit located anteriorly (Fig. 10).

Distribution.—Central Mexico, the states of Colima, Michoacan, Morelos, Nayarit, Puebla, and Zacatecas.

Material examined.—Mexico: Colima: Colima, 33 km NW, 800 m, 4 Q, on Cuphea paucipetala,



Figs 7–9. Male S3 of *Dianthidium* (*Mecanthidium*) in lateral view. 7. D. macrurum. 8. D. snellingi. 9. D. zapotecum.

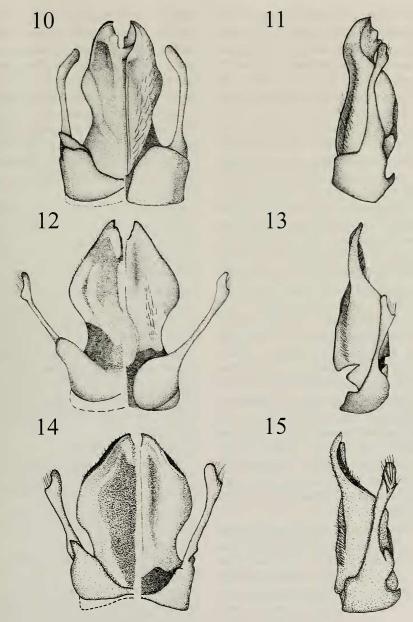
19.Jul.1989, T. Griswold (BBSL); Jalisco: Guadalajara, 2 9, 3 3, Crawford (LACM); Guadalajara, 1 &, McConnell (LACM); Guadalajara, 1 &, 15.Aug.1976, W. Hanson and M. Schwartz (BBSL); Guadalajara, 1 Q, 2.Oct.1966, G.E. Bohart and A.S. Bohart (BBSL); Guadalajara, 10 mi N, 2 ನೆ, 16.Oct.1968, G.E. Bohart (BBSL); Guadalajara, 15 mi NE, 1 ♀ and 2 ♂, 17.Sep.1970, R.M. Bohart and G.E. Bohart (BBSL); Jocotopeca, 3.4 km SE, 1493 m, 1 Q, on Cuphea procumbens, 12.Sep.1976, C.D. George and R.R. Snelling (BBSL); La Floresta, Lago de Chapala, 1510 m, 2 3, 4.Sep.1977, E. Schlinger (BBSL); La Floresta, Lago de Chapala, 1510 m, 2 Q, 4-5.Sep.1977, E. Schlinger (BBSL); Tecolotlan, 5.5 mi NE, 1 Q, 13.Sep.1982, D.K. Faulkner (LACM); Tequila, 7 km NW, 1275 m, 1 Q, 10.Sep.1974, E.M. Fisher (LACM); Tizapan El Alto, 9 km W, 1585 m, 12.Sep.1976, C.D. George and R.R. Snelling (LACM); Michoacan: Huacana, 6 km S, 600 m, 1 Q, 30 Oct. 1987, T. Griswold; Morelos: Cuernavaca, 1 3, 8.Nov.-6.Dec. 1987, F.D. Parker (BBSL); Cuernavaca, 6 mi E, 1 Q, 1.Sep.1974, G. Bohart, W. Hanson (BBSL); Cuernavaca, 10 mi E, 3 males, 15.Sep.1972, W.J. Hanson and J.M. Poff; Yautepec, 1 ♀ and 1 ♂, 13.Sep.1963, F.D. Parker and L.D. Strange; Nayarit: Ahuacatlan, 1 Q, 14.Sep.1970, G.E. Bohart and R.M. Bohart (BBSL); Ixtlan del Rio, 7 mi W, 1 3, 10.Sep.1970, E.M. Fischer (LACM); Ixtlan del Rio, 1 3, 10.Sep.1970, E.M. Fischer (LACM); Puebla: Izucar de Matamores, 9 mi W, 2 Q and 1 3, 16.Sep.1972, W.J. Hanson and J.M. Poff (BBSL); Zacatecas: Jalpa, 10 mi S, 1 &, 17.Sep.1970, G.E. Bohart and R.M. Bohart (BBSL).

Variation.—S3 in *D. macrurum* has a transverse medial process that varies in size with the size of the specimen. Large individuals have a transverse process that is taller than ½ the length of the sternum, while the height of the sternal process of small bees is considerably less than ½ its length.

Comments.—Comparison of numerous male and female specimens of putative D. macrurum and D. sonorum failed to yield characters that justify separate specific designations. The key character thought to distinguish D. macrurum from D. sonorum was the prominence of S3 (Fig. 2). A review of additional material shows a continuum in size in this structure between individuals identified as D. macrurum and D. sonorum. We find no difference in male genitalia, while there are distinct differences among other Mecanthidium species. Additionally, there is considerable overlap in the geographic distribution between D. macrurum and D. sonorum.

Dianthidium snellingi Tanner and Griswold, sp. nov.

Diagnosis.—The male of *D. snellingi* is readily identifiable by the following combination of characters: 1) a diminutive projection at the apex of T7 (Figs 3–4), and 2) a large transverse ridge across S3 (Fig. 8). The projection on the tip of T7 is broadly bifurcated and the lateral margins



Figs 10–15. Genitalia of *Dianthidium* (*Mecanthidium*) in dorsal (left half) and ventral (right half) views (10, 12, 14) and lateral profile (11, 13, 15). *D. macrurum*: 10, 11. *D. snellingi*: 12, 13. *D. zapotecum*: 14, 15.

of the tergum are broadly rounded. The anterior face of the ridge across S3 is concave, giving the distal margin the appearance of being broader than its base in lateral view. Other characters useful in identifying *D. snellingi* are: 1) penis valve in lateral view with apex narrow (Figs 12–13), 2) the interior apical margin of the

penis valve is not concave, without an anterior pit.

Male.—Color and pubescence: Face uniformly covered in simple reddish-brown setae except paraocular area; hypostomal area with long, dense, plumose setae. Vertex, genal area, and integument of paraocular area reddish-brown to light

orange. Integument of supraclypeal area, frons, and ocellar area black except small reddish-brown marks dorsal to clypeus, between antennal sockets and ventral to median ocellus. Clypeus with yellow integument apically, reddish-brown basally, apical margin black; setae longer along clypeal margin. Mandible orange with black ventral, dorsal, and cutting margins. Scape, pedicel, and first two flagellar segments of antenna mostly reddishbrown; remaining segments mostly black. Scape densely setose on basal ½. Gena densely setose with plumose setae. Integument of mesosoma mostly reddish-brown except propodeum black, and scutum with black triangle at anterior margin with apex pointing posteriorly, and thick black longitudinal sublateral marking. Scutum covered in short dense setae. Wings heavily infuscated throughout. Legs brightly reddish-brown with black markings on fore femur and on distal margins of fore tibia. Tarsi mostly orange with dense reddishbrown setae. Integument of metasoma mostly reddish-brown, T2-T7 with narrow black basal marks, dorsum covered in short decumbent orange setae. S3-S6 densely covered with long, simple, orange setae. Anterior face of transverse process with sparse orange setae. S3-S4 with long dense apical fringes.

Head.—Mandible tridentate, medial tooth low, truncate, nearer ventral than dorsal tooth. Clypeus in lateral view, distinctly convex, broadest below middle; surface deeply, contiguously punctate; punctures wider than long with dorsal margin of puncture raised making surface of clypeus appear tuberculate; punctures separated by no more than ½ × puncture width; apical margin truncate, irregularly tuberculate. Juxtantennal ridge reduced to inconspicuous angle. Malar space absent. Gena widest dorsally, maximum width approximately eye width. Vertex sharply angulate in lateral view.

Mesosoma.—Pronotal lobe lamellate, anterior margin distinctly convex. Scutum

shiny, densely but not contiguously punctate. Punctures on lateral face of mesepisternum larger than elsewhere on mesosoma, not contiguous. Preomaular area distinct, separated from lateral face of mesepisternum by omaular carina in dorsal half. Metepisternum nearly impunctate ventrally. Margin of axilla subangulate ventrally. Propodeum vertical with limited dorsal face; with large glabrous region at its distal margin extending up approximately ½ × length.

Metasoma.—T7 with rounded lateral lobe basally, apically produced into finger-like bifurcated process, with long medial carina extending length of tergum (Fig. 3). S3 with large impunctate transverse process subapically (Fig. 8); thickness in lateral view equal to ½ × length of sternum, apex wider than base in lateral view due to convex anterior face. Genitalia with penis valve not emarginate apically, thus the two valves without a visible apical opening (Fig. 12), in lateral view narrow apically (Fig. 13); gonostylus with concave apical margin, in lateral view comma shaped (Fig. 13).

Female.—Unknown

Holotype male.—MEXICO: Jalisco: Mazamitla, 3 mi NE, 12. July. 1982, D.K. Faulkner (LACM). Holotype deposited in LACM.

Etymology.—Named in honor of Roy Snelling for his great contribution to Hymenopteran taxonomy.

Distribution.—Known only from Jalisco, Mexico.

Comments.—We consider *D. snellingi* to be a morphologically distinct species from both *D. macrurum* and *D. zapotecum* based on the shape and size of the apical process on T7, the shape and size of the medial process on S3, and the thickness of the apex of the penis valve and gonostylus. *Dianthidium snellingi* has a diminutive apical process relative to *M. macrurum*, and the apex of this process in *D. snellingi* is broadly bifurcated compared to complete in *D. macrurum* and *D. zapotecum* (Figs 1, 3, 5). The medial process of S3 is large

relative to that of D. zapotecum, though there may be similar variation in its size, as seen in D. macrurum. Also, the anterior face of this process is concave in D. snellingi, making the distal margin appear broader than its base in lateral view (Fig. 8). S3 in D. macurum is not concave and gradually tapers to its apex in lateral view (Fig. 7). The apex of the penis valve of D. snellingi lacks a visible dorsal apical pit, and in lateral view it tapers gradually to its apex. The internal margin of the penis valve of *D*. macrurum is open and concave, exposing a dorsal pit; in lateral view, the apex of the penis valve is broad or swollen. The gonostylus of D. snellingi is most narrow at 1/3 of its length, in lateral view, but it lacks a basal lobe. The gonostylus of D. zapotecum also narrows significantly at 1/3 its apex, but has a prominent basal lobe.

Dianthidium zapotecum Tanner and Griswold, n. sp.

Diagnosis.—Males of D. zapotecum are easily recognized by having a diminutive apical projection on T7 (Figs 5-6) and a diminutive process on S3 (Fig. 9). T7 has obtusely angulate lateral projections and the apex of the medial process is entire. The transverse process on S3 is much smaller than that of D. macrurum and D. snellingi; its thickness in lateral view is approximately equal to 1/4 the length of the sternum. Other diagnostic characters include: penis valve with apex in lateral view narrow (Figs 14-15); interior apical margin of the penis valve not concave, without anterior pit. Females of D. zapotecum are recognizable by the combination of a concave anterior margin of the preomaular area, and axillae with lateral margins that extend beyond a line created between the lateral margins of the scutum and scutellum. In both sexes, the anterior margin of the pronotal lobe is almost in the same plane as the anterior margin of the scutum.

Male.—Color and pubescence: Face uniformly covered in simple reddish-brown

setae except paraocular area; hypostomal area with long, dense, plumose setae. Integument reddish-brown to light orange on vertex, genal area, paraocular area of face. Integument black on supraclypeal area, frons, ocellar area except small reddish-brown marks dorsal to clypeus, between antennal sockets and ventral to median ocellus. Clypeus yellow to orange with sparse long yellow setae, setae longer along black clypeal margin. Mandible orange with black ventral, dorsal, and cutting edge margins. Scape, pedicel, first two flagellar segments of antenna orange, remaining segments mostly brown. Scape setose with plumose setae on basal half. Gena densely setose with plumose setae. Scutum covered in short dense plumose setae, integument with black stripe at anterior margin extending longitudinally to middle, and small black mark anterior of axilla. Integument of axilla, scutellum reddish-brown, rest of mesosoma black to dark brown except for marginal ferrugious markings on the mesepisternum. Wings infuscated throughout. Integument of legs brightly reddish-brown with black markings on hind tibia. Tarsi mostly orange with dense reddish-brown setae. Integument of metasoma mostly reddish-brown, T2-T7 with black to dark brown basal and apical bands, dorsum covered in short decumbent orange setae. T1-T5 with medial longitudinal dark to light brown integumental stripe. S3 with anterior face of medial transverse projection with sparse orange setae. S4-S6 with plumose, silver setae, dense apical band of long, simple, silver setae.

Head.—Mandible tridentate, medial tooth angulate, nearer ventral than dorsal tooth. Clypeus deeply, densely punctate, punctures separated by no more than ½ × width of puncture, as wide as long, dorsal margin of puncture raised making surface of clypeus appear tuberculate, apical margin truncate, irregularly tuberculate. Juxtantennal ridge produced into tooth. Malar space absent. Gena widest dorsally, maxi-

mum width approximately ½ eye width. Preoccipital margin angulate in lateral view.

Mesosoma.—Pronotal lobe punctures less dense than on rest of mesosoma, not contiguous; anterior margin almost on same plane as anterior margin of scutum. Mesepisternum with distinct anterior face, separated from lateral face by carina. Outer margin of axilla subangulate posteriorly. Propodeum vertical with narrow dorsal face, with large glabrous region at its distal margin extending up approximately ½ × length.

Metasoma.—T7 with long medial carina, with lateral rounded projection (Fig. 5). S3 with small punctate transverse process situated medially; height equal to $\frac{1}{4}$ × length of sternum.

Female.—Color and pubescence: Face uniformly covered in simple yellow setae. Integument of vertex and genal area reddish-brown, paraocular area dorsally reddish-brown to yellow anteriorly. Integument of supraclypeal area, frons, and ocellar area black except quadrate reddish-brown mark between antennae and reddish-brown longitudinal band from median ocellus. Clypeus reddish-brown basally, yellow apically. Mandible reddish-brown with black ventral, dorsal, and cutting margins. Scape, pedicel, and first two flagellar segments of antenna reddish-brown; remaining segments mostly brown. Integument of scutum reddishbrown with variable black markings, frequently with central longitudinal band, lateral black band. Integument of axilla, scutellum reddish-brown, rest of mesosoma black to dark brown except for marginal ferruginous markings on mesepisternum. Wings heavily infuscated throughout. Legs brightly reddish-brown with black markings on hind tibia. Tarsi mostly yellow with dense reddish-brown setae. Integument of mesosoma mostly reddish-brown, segments T2-T7 with narrow black to dark brown basal and apical bands, dorsum covered in short decumbent tawny setae. S2–S4 with black basal bands.

Head.—Mandible edentate, apical margin with slight incurve near ventral angle, acute angle dorsally. Clypeus in lateral view distinctly convex, broadest below middle; surface deeply, contiguously, punctate; punctures as wide as long, with dorsal margin of punctures raised making surface of clypeus appear tuberculate; apical margin truncate, irregularly tuberculate. Punctures separated by as much as one puncture width. Scape uniformly covered in simple short setae. Juxtantennal ridge reduced to inconspicuous angle. Malar space absent. Gena widest dorsally, maximum width approximately eye width; densely setose with plumose setae. Vertex sharply angulate in lateral view.

Mesosoma.—Scutum punctate, covered in short, dense, stout, setae. Punctures on lateral face of mesepisternum larger than elsewhere on mesosoma, not contiguous, nearly impunctate below. Preomaular area with distinct anterior face, separated from lateral face by omaular carina on dorsal half. Outer margin of axilla subangulate laterally. Propodeum vertical with limited dorsal face; with large glabrous region distally extending approximately half length of segment.

Metasoma.—Scopa composed of long simple setae spanning S2–S5.

Distribution.—Mexico in the states of Chiapas and Oaxaca.

Type material.—HOLOTYPE: ♂, MEXICO: Oaxaca: El Camaron, 20 mi E, 21.Jul.1956, J.W. MacSwain. PARATYPES: MEXICO: Oaxaca: Cuicatlan, 4 mi N, 4900′, 1 ♂, 18.Jul.1973, R.R. Snelling; Tehuantepec, 8 km W, 3 ♀, 9–10.Aug.1974, E.M. Fisher and J.L. Fisher; Chiapas: El Aquacero, nr Ocozocoautla, 1 ♀, 26.Oct.1986, E. Fischer and D. Thomas; 1 ♀, Tuxtla Gutierrez, 26.Jul.1987, F.D. Parker. Holotype deposited in CISC; paratypes deposited in BBSL, CISC, and LACM.

Variation.—Males vary in integumental color, particularly on the mesosoma which varies from tawny to dark reddish-brown.

There is also some variation in the color of the mandibles from light tawny to orange, and the size and position of the black integumental markings of the scutum. There seems to be little variation, however, in the size and shape of the apical process of T7 and the medial process of S3. Females also vary in integumental color, most notably on the mesosoma. Individuals with dark mesosoma appear to have darker and more robust medial bands on the terga.

Comments.—Dianthidium zapotecum is morphologically distinct from both D. macrurum and D. snellingi in the shape and size of the apical process on T7, the shape and size of the medial process on S3, and the thickness of the apex of the penis valve and gonostylus. The apical process on T7 of D. zapotecum is diminutive relative to other Mecanthidium and the apex does not bifurcate, as it does in D. snellingi. In lateral view the anterior face of the process is not concave, as in D. snellingi, and does not taper, as in D. macrurum. The penis valve of D. zapotecum is not swollen, as in D. macrurum, and the gonostylus has a basal lobe that is absent in D. snellingi. The geographical distribution of D. zapotecum appears to be disparate from either D. macrurum or D. snellingi. Dianthidium macrurum is distributed across central Mexico from the western coastal states of Colima,

Michoacan, and Nayarit to the central states of Puebla and Zacatecas. *Dianthidium snellingi* has been collected in the center of this distribution in the western coastal state of Jalisco. *Dianthidium zapotecum* is only known from the southern states of Oaxaca and Chiapas.

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